Protist taxonomic and functional diversity in soil, freshwater and marine ecosystems

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**Article Info**

Handling Editor: Frederic Coulon

Keywords:
Terrestrial systems
Metabarcoding
Microbial eukaryotes
Taxonomic and functional diversity
Ocean

**Abstract**

Protists dominate eukaryotic diversity and play key functional roles in all ecosystems, particularly by catalyzing carbon and nutrient cycling. To date, however, a comparative analysis of their taxonomic and functional diversity that compares the major ecosystems on Earth (soil, freshwater and marine systems) is missing. Here, we present a comparison of protist diversity based on standardized high throughput 18S rRNA gene sequencing of soil, freshwater and marine environmental DNA. Soil and freshwater protist communities were more similar to each other than to marine protist communities, with virtually no overlap of Operational Taxonomic Units (OTUs) between terrestrial and marine habitats. Soil protists showed higher γ diversity than aquatic samples. Differences in taxonomic composition of the communities led to changes in a functional diversity among ecosystems, as expressed in relative abundance of consumers, phototrophs and parasites. Phototrophs (eukaryotic algae) dominated freshwater systems (49% of the sequences) and consumers soil and marine ecosystems (59% and 48%, respectively). The individual functional groups were composed of ecosystem- specific taxonomic groups.

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https://doi.org/10.1016/j.envint.2020.106262
Received 7 May 2020; Received in revised form 31 October 2020; Accepted 2 November 2020

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1. Introduction

Assessing patterns of biodiversity — how they vary among taxonomic groups, biomes and ecosystems — is an old (Wallace, 1876) but still relevant question in biology (Gaston, 2000; Mora et al., 2011; Titensor et al., 2010; Wall et al., 2001) that provides a starting point to understand ecosystem functioning and their associated services provided by the organisms living there (Cotterill et al., 2007). Most diversity on Earth is microbial, and protists seem to form a substantial part of this diversity (Adl et al., 2019). Estimating protist diversity is, however, challenging because protists are mostly small and inconspicuous. Environmental DNA-based methods have revealed a high and largely unknown taxonomic diversity of both prokaryotic (Delgado-Baquerizo et al., 2018) and eukaryotic microorganisms (de Vargas et al., 2015; Tedesco et al., 2014).

Protists play critical roles in Earth’s systems; for instance marine photosynthetic protists (the eukaryotic part of phytoplankton) fix as much carbon as all terrestrial plants together (Falkowski et al., 1998). Still heterotrophic protists, including many uncharacterized parasitic and mutualistic symbionts, have recently been shown to be even more diverse and abundant than their phototrophic counterparts (de Vargas et al., 2015; Lima-Mendez et al., 2015; Seeleuthner et al., 2018). Freshwater systems, with their wide variation in physical and chemical properties may host drastically different communities (Boenigk et al., 2018; Debroas et al., 2017), and soil protists may champion biodiversity due to the complex and highly dynamic distribution of water in soil pores that creates extremely heterogeneous environments in time and space. This constant change of conditions promotes the activity of only a part of the microbial community, while the rest remains inactive. This mechanism has been suggested to be key in promoting high microbial diversity in prokaryotes (Tecon and Or, 2017), and similar mechanisms have also been suggested for protists (Velasco-Gonzalez et al., 2020).

Pioneering studies of soil protists diversity encompassing limited geographical areas and soil types, have revealed an extreme level of an unknown diversity. Indeed as shown in three neotropical forests, only 8.1% of all sequences had ≥95% similarity with known references sequences (Mahe et al., 2017). How these organisms relate to those encountered in the better-known aquatic systems can help in better understanding the diversity and functioning of soil protists. Thus, there is a need for studies integrating as many ecosystems as possible. Of particular relevance to environmental microbiology is knowing which groups contribute to the taxonomic and functional diversity in each ecosystem, how do overall diversity compare and how variable it is in each ecosystem (Geisen et al., 2017).

This study compares the diversity of protists across the marine and freshwater sunlit and top soil ecosystems. Using both published and new data from the same genetic marker and sequencing technology (Illumina high-throughput sequencing of the v9 region of the 18S rRNA gene), our data from the same genetic marker and sequencing technology (Illumina high-throughput sequencing of the v9 region of the 18S rRNA gene), our还有什么未标注的区域或者需要注释的地方呢？
r.pl). Sequences from all samples were then dereplicated with a custom script (https://github.com/cseppey/bin_src_my_prog/blob/master/cpp/derep.cpp) prior to OTU clustering performed with swarm v2.1.13 with the fastidious option (Mahe et al., 2015). OTUs were finally assigned using the global alignment option on vsearch v2.4.4 (Rognes et al., 2016) against the PR database v4.12.0 (Guillou et al., 2012). Chimerical sequences were removed by comparing the reads within the dataset with the program vsearch v2.4.4 (Rognes et al., 2016).

Certain OTUs were then sorted out according to three criteria, as originating from putative non-protoplasts and macroscopic organisms: 1) OTUs belonging to Metazoa, Embryophyceae, Fungi and Rhodophyta were removed, as well as 2) the ones having a sequence with a length below 100 nucleotides, and 3) the ones having a percentage of identity below 60% with the database as putative prokaryotes.

2.4. Functional assignment of OTUs

We assigned OTUs to three major functional groups, based on their taxonomic affiliation according to three main trophic modes: Photo trophic (Archaeplastida, Ochrophyta), Parasitic (Apicomplexa, Icthyosporea, MALV, Peronosporomycetes, Syndiniales), Consumers (Ciliophora, Rhabdaria, non-Fungi Opisthokonta, Amoebozoa, non-Ochrophyta and non-Peronosporomycetes Stramenopiles) (Table F.1).

We considered as phototrophic any organism that used photosynthesis, independently of the capacity of the organism to also retrieve carbon through heterotrophy (mixotrophy). The organisms that acquired food through phagocytosis were labelled consumers. We decided to consider as parasite any symbiont reducing the fitness of its host, independently if the host is killed by its symbiont (parasitoid) or not. We also consider all Peronosporomycetes as parasites because parasitism is considered as the ancestral condition of the group (Misner et al., 2014), even though many of them often live as saprotrophs and behave as facultative parasites.

We verified manually the precise phylogenetic affiliation of all Dinophyceae OTUs to infer their function. However, 55% of dinokaryotic OTUs were still assigned to “unknown Dinophyceae” which prevented functional assignment. These organisms may range functionally from phototrophic to strictly heterotrophic consumers. In marine systems, it has been estimated that 58% of species are strictly consumers while 42% perform photosynthesis. In freshwater systems, only 12% are consumers while 88% are phototrophic (Gómez, 2012). As phototrophy is a trait that changes rapidly in dinokaryote evolution (Saldarriaga et al., 2004), we considered that these numbers represented both the percentage of OTUs and of reads in both marine and freshwater systems. Soil dinoflagellates have been poorly described, but our results show more similarities with freshwater communities than with marine samples; therefore, we considered also that 12% of soil dinoflagellates were consumers (Fig. A.1).

Chrysophyceae present different nutrient acquisition strategies ranging from phototrophic to consumers (Boenigk et al., 2005). Recent works suggest that Chrysophyceae are ancestrally phototrophic, some groups or species having lost photosynthetic ability later during their evolutionary history (Dorrell et al., 2019). We considered as consumers those OTUs assigned to Chromulinosphaera, Segregatosphaeria, Otkomonas (Clade B2), Acrispumella, Apoikia, Edaphospumella, Kephyrin, Spumella, and Poteriopumella (Clade C), as well as the Clade F (Nematophyllum and allied genera). The rest were considered as phototrophic. As for the Dinophyceae, many Chrysophyceae OTUs were not functionally assignable (44% of the OTUs of the first bootstrap). To our knowledge, there is no information on the consumer/phototrophic ratio for this clade as it is for Dinofyceae in marine and freshwater. In order to include the functionally unknown Chrysophyceae, we calculated the ratio consumer/phototroph for the functionally assigned OTUs in each sample. Then, we pooled reads and OTUs number of functionally unclassified Chrysophyceae according to the ratio consumer/phototroph.

Our sampling design did not allow us to assess temporal patterns such as algal blooms, increasing the proportion of phototroph, parasites developing on the algae or consumers feeding on the soluble organic matter left after the parasitic infection. In addition, certain groups of species can switch rapidly between different trophic lifestyles. Nevertheless, the overall signal can provide an insight of the importance of each function in the different ecosystems.

2.5. Statistical analyses

In order to avoid bias related to 1) the number of samples per ecosystem and 2) the sequencing depth, we ran the analyses on 100 bootstraps composed of 60 samples (20 samples per ecosystems) of 10'000 reads each. The figures were selected from a bootstrap best representing the overall trend among the 100 bootstraps (Annex H1-5). We acknowledge that our conservative sequence cutoff to 10'000 reads per sample is far from complete taxon sampling. Yet, we here did not aim to obtain complete species inventories but rather to enable reliable community comparisons of the numerically dominant taxa across ecosystems.

We estimated the γ diversity of each ecosystem with the bootstrap estimator of species richness (BES) and a species accumulation curve (SAC) (functions specpool and specaccum, package vegan v. 2.5–2 (Oksanen et al., 2018)). We also estimated the α diversity (Shannon index, function diversity, package vegan v. 2.5–2, (Oksanen et al., 2018)) of each of the 55 major lineages that represent the bulk of the known protist diversity in each type of ecosystem, respectively, following the same procedure as described above.

We assessed the similarity patterns among protist communities (β-diversity) by non-metric multidimensional scaling (NMDS). NMDS was calculated on Bray-Curtis dissimilarities retrieved from the sequence relative abundance. The significance of differences between pairs of ecosystems were measured by permutation tests (10’000 permutations; functions vegdist, metaMDS and envfit, package vegan v. 4.3. (Pohliert, 2014)) in each bootstrap. We also use this approach to test the differences between ecosystems for the log of the number of reads, the log of the richness and the Shannon diversity within each of the 55 dominant taxonomic groups, as well as for the functional groups relative abundance.

2.6. Dataset consistency

This study is, to a certain extent, a meta-analysis because part of the data (concretely, the marine data) was derived from other studies. Thus, most samples were obtained with distinct methods. Thus, despite targeting the same rRNA region (V9) and using the same sequencing technology (Illumina sequencing) the sampling and laboratory procedures used were not homogeneous, thus potentially producing biases. We therefore tested how robust our data was to methodological biases, including (1) different filtration and sample preservation protocols (2) use of different extraction kits and (3) use of different primer sets.

(1). Pore filter sizes varied between freshwater and marine samples. In both cases, filter mesh sizes are below 1 μm, which corresponds to the size of the smallest eukaryotes known, such as for instance Ostreococcus tauri (Chrietienot-Dinet et al., 1995). We are confident, therefore, that we retrieved all eukaryotes in the water column, and therefore are comparable to soil in the range of sizes that were considered.

(2). Extraction kits differed between freshwater/soil and marine samples. While it has been shown that slightly different protist
community profiles were retrieved by using commercial and “homemade” protocols, the differences concerned only particular groups (Santos et al., 2017). Given the differences that have been shown between marine and freshwater/soil communities, it is difficult to evaluate how far this bias affects the big picture presented here as retrieved with two commercial kits, but differences are most likely minor.

(3). Primer sets differed between freshwater/soil and marine samples. However, these two sets amplify the same spectrum of the eukaryotic diversity (Geisen et al., 2019). We tested this assumption in silico from data that used the primers on the same samples (Amaral-Zettler et al., 2009; Stoeck et al., 2009) to demonstrate that biases produced by different primer sets were negligible (Appendix I).

3. Results and discussion

3.1. Communities richness: \( \alpha \) and \( \gamma \) diversity

As expected, protist \( \gamma \) diversity predicted by BES was higher for soils (16’337 OTUs \( \pm \) 892 SE) than for the two aquatic ecosystems (freshwater: 11’490 OTUs \( \pm \) 756, marine water: 12’540 OTUs \( \pm \) 689) (Fig. 1A, Table H.1). Gamma diversity was highest in soils in 26.3 \( \pm \) 0.1 of the taxonomic groups, 11.0 \( \pm \) 0.1 in marine samples and 11.7 \( \pm \) 0.1 in freshwater (Fig. 2, B.1). Even though OTU richness did not reach saturation, most of the SAC trends clearly discriminated the gamma diversity of the three ecosystems; trends that would likely stand with a deeper sampling effort (Fig. B.1).

Freshwater had the lowest \( \alpha \) diversity (3.68 \( \pm \) 0.18 SE), while soils and marine waters did show significantly difference, soil being slightly more diverse (respectively, 5.25 \( \pm \) 0.22 SE and 5.05 \( \pm \) 0.08 SE) (Fig. 1B, Table H.1).

In line, 20.67 \( \pm \) 0.28 out of 55 broad taxonomic groups targeted showed significantly higher \( \alpha \) diversity in soils while 9.15 \( \pm \) 0.8 were more diverse in marine samples and 0.90 \( \pm \) 0.05 were more diverse in freshwater (Fig. B.2). This probably higher \( \alpha \) diversity in soils followed our prediction based on the co-existence of several dormant and active organisms that differ in their ecological requirements but reactivate under suitable conditions.

The high \( \alpha \) and \( \gamma \) diversity in soils contrast with the low number of described soil protist species (ca. 21’000 species (Mora et al., 2011)), while estimations suggest the existence of millions (Geisen et al., 2018). We compared the level of knowledge for all three ecosystems based on the percentage of identity between the OTU reads and the best match with the PR\(^2\) eukaryotic ribosomal database (Guillou et al., 2012) (Fig. C.1, Table H.2). Soil OTUs had, on average, a significantly lower percentage of similarity with known sequences (87.28% \( \pm \) 0.08 SE) than freshwater systems OTUs (90.56% \( \pm \) 0.08 SE), with the best percentage of identity with the database for the OTUs found in marine ecosystems (91.39% \( \pm \) 0.09 SE, Nemenyi test: \( P < 0.05 \)).

3.2. Community heterogeneity; \( \beta \) diversity

\( \beta \) diversity was highest in freshwater (0.924 \( \pm \) 0.006), slightly but significantly lower in soils (0.894 \( \pm \) 0.006) and lowest in the marine plankton (0.777 \( \pm \) 0.009) (Fig. 1C, Table H.1). This higher biological heterogeneity in freshwater and soil systems reflects their respective heterogenous abiotic conditions compared to the relatively buffered conditions in the ocean. Indeed, soil and freshwater samples vary considerably in their pH values which has a known impact on microbial diversity.
Fig. 2. Schematic phylogenetic tree of the main protist taxa and their relative abundance in three ecosystems (marine water: dark blue, freshwater: cyan, soil: orange). Barplots represent the OTU richness of each taxon predicted by bootstrap estimator of species richness in each ecosystem. Predictions higher than 500 OTUs are written numerically. Numbers in front of bars indicate significantly different groups (Nemenyi test $P < 0.05$), “1” representing the highest distribution and “3” the lowest. Pie-chart represent the relative abundance of reads in function of each ecosystem (marine water: dark blue, freshwater: cyan, soil: orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
3.3. The distribution of taxonomic and functional diversity

Consumers dominated sequence relative abundance in soil (Fig. 3, Table H.3). While rhizarians in terrestrial systems (freshwater and soil) were dominated by Cerozoa, marine rhizarians mostly belonged to Radiolaria (Fig. E.2). Ciliates were overall, respectively, the richest and second richest group of consumers in freshwater and soil ecosystems and show the same pattern for relative abundance (Fig. E.2). Their broad range of lifestyles is key to their evolutionary success in many ecosystems (Lynn, 2008) although their highly polyplid macronuclei might somehow artificially inflate their estimated abundance in the environment (de Vargas et al., 2015). Stramenopiles constituted the third most represented major group of consumers overall (Fig. E.2). Non-photosynthetic Stramenopiles included organisms collectively known as MAST (Massana et al., 2004) (Marine STramenopiles, now known to also thrive in other ecosystems), Bicoecea and Labyrinthulomycetes. Labyrinthulomycetes were previously considered largely marine until new deep-branching phototrophic groups were discovered in other ecosystems (Gomaa et al., 2013). Our data confirm their prevalence in soil, as they present even higher α and γ diversity in these systems (Fig. B.1-2).

Phototrophs were overall the second most abundant functional group, and dominated freshwater systems (Fig. 3, Table H.3). Interestingly, their relative abundance in marine plankton was not significantly higher than in soil (Fig. 3, Table H.3, Nemenyi test: P > 0.05). Given the importance of phototrophy in marine systems for global carbon fixation and nutrient cycling (Falkowski et al., 1998), this relative abundance suggests a remarkable role in microbial photosynthesis in soils. Although the standing biomass of soil phototrophs (“subaerial algae”) is negligible compared to plants, their turnover can occur much faster and accelerated by specific predation (Mann and Vanomelingen, 2013; Seppey et al., 2017), as is well documented in the ocean. Mostly photosynthetic dinoflagellates were extremely abundant in marine systems while Chrysophyceae dominated the freshwaters and Archaeplastida were widespread in soils (Fig. E.3). Interestingly, the main freshwater phototrophic groups (phototrophic Chrysophyceae, Cryptophyta, phototrophic Dinofyceae) behave also alternately as consumers (mixotrophs). In soils, these groups are way less represented, with the groups being present often having lost the capacity for photosynthesis (such as Clade C Chrysophytes, collectively designated as Spumella spp. (Boenigk et al., 2005). Hence, in freshwater systems the number of strict consumers seems lower than in other systems, but this role may be assumed to some extent by mixotrophic phototrophs. Many dinoflagellates and Archaeplastida often form mutualistic associations with other protists, but also fungi and animals (LaJeunesse, 2001). Their high abundance agrees with the immense importance of photosymbiosis at a global level.

Parasitic taxa represented roughly 15 to 20% of all sequences in marine and soil systems, but only around 5% in freshwater systems (Fig. 3), where taxa of the fungal phylum Chytridiomycota likely fill the ample niche of eukaryotic parasites (Rasconi et al., 2012). Chytrids are indeed generally well represented in environmental DNA-based diversity surveys (Debroas et al., 2017; Lepere et al., 2019). In soils, genuine parasites (who did not necessarily kill their host) were dominated by Apicomplexans, an extremely diverse and abundant group known to infect Metazoans (Mahé et al., 2017; Singer et al., 2020), and plant parasites such as many terrestrial oomycetes and plasmidophorids (Fig. E.4). In marine systems the parasitoid strategy (in which the host is killed to complete its life cycle) dominates with an overwhelming relative abundance of Syndiniales, which lyse host cells before spreading propagules (Fig. E.4). Freshwater systems comprised parasitoid groups such as Perkinsea, Syndiniales and most certainly Chytridomyctisea (Sime-Ngando et al., 2015), but also “true” parasites like Peronosporomyctisea, Apicomplexa and Ichtyospora (Fig. E.4). This suggests a high connectivity of terrestrial systems with the macroscopic food web (plants and animals) whereas in aquatic systems (freshwaters and marine waters) parasitism would affect mostly other microbes that would be rapidly lysed, thus creating bloom dynamics which may accelerate the pace of nutrient turnover (Mangot et al., 2013).
longer lifespan of macroscopic organisms and the fact that these might not be systematically killed by their parasites suggests different nutrient transfer through the systems.

In spite of all differences observed among the three ecosystems, our survey revealed a remarkable functional homogeneity. Heterotrophy dominates all processes in general, taking into account that even in freshwater where the proportion of phototrophs is higher, many pigmented organisms are actually mixotrophic (i.e., combining phagotrophy and photosynthesis (Sanders, 1991)). Phototrophs appear in lower proportions, their standing biomass probably constrained by intense predation enhancing nutrient turnover. The action of parasites also likely contributes to nutrient turnover, by lysing microbial cells through a parasitoid strategy in aquatic ecosystems and increasing the death rate of macro-organisms in terrestrial ecosystems.

3.4. Conclusions

A key result of our study is that soils host the richest protist communities on Earth. Thus, while all ecosystems contain a wealth of understudied protist species, this is especially true in soils. In line with our predictions, spatial and ecological heterogeneity are correlated with diversity, as shown by the higher β diversity observed in freshwater and soil environments. This calls for an increased exploration of less prospected ecosystem types to find new diversity following by the expansion of the existing curated and annotated databases such as UniEuk (Berney et al., 2017).

Our estimations for functional diversity were only partially fulfilled. On one hand, our study underlines the importance of phagocytosis through the relative abundance and diversity of consumers in all ecosystems, and especially in soils. On the other hand, the amount of photosynthesizing organisms were not significantly different in marine systems, and especially in soils. On the hand, the amount of phototrophs is higher, many pigmented organisms are actually mixotrophic (i.e., combining phagotrophy and photosynthesis (Sanders, 1991)). Phototrophs appear in lower proportions, their standing biomass probably constrained by intense predation enhancing nutrient turnover. The action of parasites also likely contributes to nutrient turnover, by lysing microbial cells through a parasitoid strategy in aquatic ecosystems and increasing the death rate of macro-organisms in terrestrial ecosystems.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envint.2020.106262.

References


